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EXPERIMENTS ON MIMICRY IN CUBA, WITH SUGGESTIONS FOR FUTURE STUDY

By P. J. Darlington, Jr.

(*Museum of Comparative Zoölogy, Cambridge, Mass.*)

Communicated by Dr. G. Salt, F.R.E.S.

(Read 1st June, 1938.)

With Plate 1.

In 1924, through the generosity of Mr. Edwin F. Atkins, Harvard University opened a laboratory for biological research on the Atkins sugar estate, "Soledad," near Cienfuegos, Santa Clara Prov., Cuba. Among the first students to use the laboratory were two entomologists, J. G. Myers and George Salt, who later published, as one of the results of their visit, a paper (1926) describing several possibly mimetic associations of ants and ant-like arthropods. Since then I have myself been fortunate enough to visit Soledad four times.* My interest was aroused by Myers' and Salt's paper, and I have watched constantly for the ant-like forms described by them and for other organisms which might be mimics, and during my last visit I had time to make a few experiments. The results were unexpectedly significant. I believe that further experimentation is very much worth while, and I shall make some suggestions for it later in this paper. The Soledad station is endowed, and several students go there every year. It ought to be possible, in the course of time, for a succession of observers to accumulate more information about single examples of mimicry than has ever been done before. As a preliminary contribution I shall describe here not only my experiments, but also, in some detail, the organisms with which the experiments were made and their environment.

I am indebted to the late Dr. W. M. Wheeler and to Dr. Thomas Barbour for reading the manuscript of this paper and for suggestions, to Mrs. Edwin F. Atkins for contributing the cost of painting the coloured plate, and to Mr. E. N. Fischer for the pains he has taken in the painting of the plate. The cost of reproduction has been defrayed by a grant authorised by Prof. G. D. Hale Carpenter from the fund for promoting the study of organic and social evolution presented to the University of Oxford by Prof. J. Mark Baldwin.

In the simplest theoretical example of Batesian or pseudaposematic mimicry there are three elements: an inherently inedible *model*, an edible *mimic* which escapes being eaten as a result of its resemblance to the model, and a *predator*. Simple Müllerian or synaposematic mimicry differs from Batesian mimicry in that model and mimic (if they can be called such) are both inedible; both, however, as a result of their mutual similarity, obtain increased protection from a predator. The predator is as essential to Batesian or Müllerian mimicry as the model or mimic. Without a predator, mimicry is pointless; it is the activity of the predator which presumably causes the evolution by selection of the mimetic characters in the first place. Since it is awkward constantly

* October to December, 1926; June, 1929; August, 1932; and April, May, and part of August, 1936.

to refer to a " predator affecting mimicry " or " a predator inducing mimicry," it will be convenient to call such a predator a *mimefactor* or mimic-maker.

In ideally simple examples of mimicry, mimefactor, model, and mimic occur in approximately the same environment and at the same season. All should be diurnal, if the mimicry is of form or colour, for details of form and colour are presumably less apparent at night. The mimefactor must have special characteristics: it must be reasonably common, must depend upon sight rather than scent, unless the mimicry is of odour or texture, and must be discriminating in its choice of food. In Batesian mimicry, the model must be common; the mimic, as a rule, less so. Granted that mimicry occurs at all, many variations and imperfect approximations are to be expected, but the conditions enumerated in this and the preceding paragraphs are those for which supposed examples of mimicry should first be tested.

The following check-list sets forth in natural order the more important points to be considered in describing and testing cases suspected of mimicry.

Check-List of Items for Reference in Describing and Testing Examples of Mimicry.

Environment: list of possible mimefactors.
Mimefactor(s): brief description;
habitat, season, and abundance;
whether diurnal;
senses, especially relative importance of sight;
range of food, and discrimination shown.
Model(s): appearance and behaviour;
habitat, season, and abundance;
whether diurnal;
protective adaptations, if any;
acceptability to mimefactors.
Mimic(s): appearance and behaviour;
habitat, season, and abundance;
whether diurnal;
protective adaptations, if any, besides mimicry;
direct relation (if any) to models (*e.g.* as guests);
acceptability to mimefactors;
acceptability of related but differently coloured forms, or of mimics disguised or fed artificially.

Of the numerous examples of apparent mimicry among insects and spiders near Soledad, the most striking and the one which lends itself best to experiment centres around the brilliantly coloured Lycid beetles of the genus *Thonalmus*. These, and other beetles of different families which resemble them, are the chief subjects of the present paper.

The Environment.

The species of *Thonalmus* are found chiefly in scrubby or semi-open places —borders of woods, the hedgerows formed by living fence posts which are so common in Cuba, and broken second-growth woodland. The insects rarely enter deep forest or open fields. They are found in shrubbery, not, except by accident, upon the ground. They are diurnal.

The environment of any organism is a very complex thing and very difficult to analyse. In the present case, however, it is possible to go farther towards an analysis than might at first be supposed, for the Cuban fauna is an insular one much less diverse than that of an equal area in the continental tropics. The object of analysis is, of course, to discover predacious organisms which might act as mimefactors on adult, diurnal beetles of the size of *Thonalmus*, from $\frac{1}{4}$ to $\frac{1}{2}$ inch in length.

Parasites may probably be ruled out on account of their usual preference for immature stages. Nocturnal predators may probably be ruled out too. Strictly terrestrial predators may be ruled out because *Thonalmus* lives above the ground. Predators which are uncommon may be ruled out as not likely to be important. What predators, then, remain?

There are no native mammals of importance—the bats, of course, are nocturnal. Migrant birds may probably be ruled out, for they visit Cuba chiefly during the dry season when the beetles which resemble *Thonalmus* (but not *Thonalmus* itself) appear usually to be in the larval stage. A number of native birds, however, are diurnal and insectivorous and some of them are more or less common about the shrubbery where *Thonalmus* occurs.* Lizards are numerous near Soledad, but only two species, *Anolis sagrei* (Duméril & Bibron) and *Anolis porcatus* Gray, are common and active by day in the habitat of *Thonalmus*. The others are strictly forest species, or nocturnal, or confined to the ground, or uncommon. There are no diurnal arboreal frogs near Soledad. There are, of course, various predacious insects. They include a number of hunting wasps, but probably none of them is important in the present connection.† Predacious beetles are numerous, too, especially the CARABIDAE, but probably none of the common arboreal species is large enough to attack prey the size of *Thonalmus*. Two or three MANTIDAE occur in central Cuba, but I think none is common enough to be worth consideration. Predacious flies, especially ASILIDAE,‡ are commoner, however, and there are a number of

* The species most worthy of attention are the Ani, *Crotophaga ani* L.; the Cuban Lizard Cuckoo, *Saurothera merlini* d'Orbigny; the Cuban Tody, *Todus multicolor multicolor* Gould; the Gray Kingbird, *Tyrannus curvirostris curvirostris* (Hermann); three small flycatchers, *Tolmarchus caudifasciatus* (d'Orbigny), *Myiarchus sagrae sagrae* (Gundlach), and *Blacicus caribaeus caribaeus* (d'Orbigny); the Cuban Mockingbird, *Mimus polyglottus orpheus* (L.); two vireos, *Vireo gundlachii* Lembeye and *Vireo calidris barbatula* (Cabanis); and perhaps the Cuban Oriole, *Icterus hypomelas* (Bonaparte).

† Dr. Richard Dow, who has collected and observed wasps at Soledad and whose speciality is the wasps' prey, wrote me, "... I do not know of any Cuban records of wasps preying on Coleoptera, either in collections or the literature. Such records are likely to be scarce for any region. Since we are concerned with adult Coleoptera, there are only two genera of aculeate wasps that are likely to serve as predacious enemies: *Cerceris* and *Microbembex*. ... *Cerceris* usually preys on beetles, though a few species take bees. Most of the recorded victims are CURCULIONIDAE, but the following families are represented in decreasing numbers: BUPRESTIDAE, CHRYSOMELIDAE, BRUCHIDAE, NITIDULIDAE, PHALACRIDAE, TENEBRIONIDAE, CERAMBYCIDAE (LAMIINAE), and ANTHRIBIDAE. [The CERAMBYCIDAE is the only one of these families which contains *Thonalmus*-like species.] Six species of *Cerceris* have been described from Cuba. ... *Microbembex* [one species in Cuba] preys indiscriminately on a wide variety of insects, including beetles. It takes not only living prey, but disabled and dead arthropods as well. ... I doubt if any sphecoid wasp is sufficiently specific in its choice of prey to have caused its victims to mimic protected forms."

‡ At Rio Frio, south of Santa Marta, Colombia, 8 January, 1929, I saw an Asilid fly catch a small black and red Lycid in the air, but immediately release it. I was not able to capture either insect. This brief observation suggests that neotropical ASILIDAE sometimes prey on beetles the size of LYCIDAE, but that the LYCIDAE themselves are not taken.

predacious Hemiptera, especially REDUVIIDAE, which may be important, although I have little information about them. Dragonflies, too, are common and must be taken into account. Finally, of course, there are spiders.

There seem, then, to be near Soledad only the following predacious organisms which are likely to be important mimefactors affecting beetles of the size and habitat of *Thonalmus* : less than a dozen birds; two lizards; a few insects such as ASILIDAE, REDUVIIDAE, and dragonflies; and spiders. This list could probably be reduced if the food habits of the various organisms were better known.

Of these organisms, the two lizards are best suited for cage experiments. Moreover, I believe from random field observations that they are actually the most important insectivorous animals in *Thonalmus'* habitat, and those most likely to be mimefactors. Of the two, *Anolis sagrei* is the commoner and occupies an environment more nearly coinciding with that of *Thonalmus*. *Anolis sagrei* was, therefore, selected for experiment.

Anolis sagrei (Duméril & Bibron).

Anolis sagrei is a rather generalised lizard, except that its toes are dilated for climbing. Adult males are six or seven inches long; females, smaller. The tail accounts for about $\frac{5}{8}$ of the length in perfect specimens. The male is grey or brown or blackish above, either nearly uniform or with variable inconspicuous marks. The female is similar in ground colour but usually has a light dorsal line or series of light dorsal rhombic markings. Both sexes are pale below. The male possesses a longitudinal dewlap under the throat which is concealed in repose, but which can be fanned outward and forward at will. The dewlap is of orange-red skin with scattered black scales and a yellow margin, and is the most useful diagnostic character of the species.

The habitat of *Anolis sagrei* is almost exactly the same as that of *Thonalmus* —forest borders, hedgerows, and other bushy places. Its place is taken by other species of *Anolis* (especially *A. homolechis* Cope) in heavy forest, and by ground-living lizards of other genera in open places. Within its habitat, *A. sagrei* is very common indeed at all seasons, "one of the commonest lizards in the world where it occurs," according to Barbour & Ramsden (1919, p. 143). Individuals may often be seen on the ground and frequently drop to the ground and run into hiding when alarmed, but the species belongs essentially to the shrub-and-tree-trunk zone of arboreal life. Males commonly cling head downward on sunny trunks or fence posts, pumping themselves up and down energetically at intervals and flashing their brilliant dewlaps, and, if an observer will stand quietly, he will see individuals of both sexes and all sizes slipping actively along horizontal limbs and root buttresses, leaping from one sapling to another, or hunting in shrubbery.

These lizards are strictly diurnal. In the evening they crawl out among the leaves at the very tips of branches (perhaps to escape snakes) and spend the night flat and motionless, with their eyes closed. I have seen many of them sleeping in this way in the wild state. In cages, the lizards withdraw into corners to sleep.

As to their senses, the vision of *Anolis* is excellent. I have several times seen individuals travel twelve or fifteen feet to investigate slight movements among the leaves or to reach another lizard, and the precision with which they leap two or three feet from one tree trunk to another is significant. They hunt by sight, too, for they frequently capture their prey (which they seize directly in

their mouths) by sudden direct rushes from a distance of several inches or a foot. On the other hand, I believe that they have practically no sense of smell. I have never seen them nose at objects as though smelling them.

Anolis sagrei feeds chiefly (possibly entirely) on living insects, although individuals may be force-fed successfully with meat. The lizard is not, however, indiscriminately insectivorous. My caged individuals ate most readily soft, immature wood roaches (*Pycnoscelus surinamensis* (L.))* and slender, green, Geometrid-like lepidopterous larvae.† They accepted house flies, and I have seen uncaged *Anolis* eat small crickets. The caged specimens took readily, too, medium-sized beetles, as large as or larger than *Thonalmus*, of the families ELATERIDAE, SCARABAEIDAE, and CERAMBYCIDAE. The *Anolis* held the beetles crosswise in their mouths and chewed them for from a few seconds to two or three minutes before swallowing them. Sometimes, when there was more than one lizard in a cage, a male would stop chewing long enough to raise his head and flash his dewlap warningly, without, of course, releasing the insect. Sometimes the beetles' elytra were broken off and dropped during the chewing process, but this was apparently accidental, for the elytra and other hard parts of medium-sized beetles pass readily through the lizard's digestive tract and are eliminated with the faeces.

In contrast to the variety of insects which they would accept, my caged lizards refused to eat Hemiptera, not only those with a powerful "stink," but also those which were virtually stinkless.‡ They refused also large beetles such as *Phyllophaga baraguensis* Chapin (a June bug) an inch long and *Pyrophorus havaniensis* Cast. (a light-bearing click-beetle) of the same length.

The *Anolis* adapted themselves quickly to captivity. The cages I used were rectangular, 14½ inches long, 9½ wide, and 10½ high. Tops and walls were of wire screen; the floors, solid. The lizards were caught by hand and carried to the laboratory in small pocket cages. Two of the first lot copulated within an hour of the time they were brought in. They fed readily, and eventually learned to come to attention when I opened the cage door to put in food.

* This insect is probably a staple food of *Anolis sagrei* in the wild state. On several occasions, when I have been collecting insects by washing out trash on the banks of streams, wild *Anolis* have come down to the bank and caught immature roaches which I had allowed to escape.

† Wild *Anolis*, when caught, frequently have smooth lepidopterous larvae in their mouths or throats.

‡ The lizards were offered four species of Hemiptera. First, *Dysdercus andreae* (L.), a rather slender, soft, red and black bug about 10 mm. long. This bug has characteristic stink but no armament of spines, and does not try to defend itself with its beak. Two specimens were placed in a cage with two male and one female *Anolis sagrei*, which had no other food. The bugs were very active, constantly running and flying, but the lizards paid no attention to them. After 24 hours, with the bugs still untouched in the cage, I put in some acceptable insects which the lizards ate at once. On another occasion three other species of bugs were placed in the cage with the same individuals of *Anolis*. The bugs were *Euryophthalmus sellatus* (Guér.) (moderately slender, soft, black and cream coloured, slightly larger than the *Dysdercus*, without spines, and with no obvious stink), *Edessa bifida* (Say) (hard, broad, brownish-green, 12 or 13 mm. long, without spines but with a strong stink), and *Hymeniphera lobata* (Burm.) (moderately hard, rather slender, dark brownish, 12 or 13 mm. long, with small spines at the sides of the prothorax but no stink). (None of these bugs was observed to use its beak for defence.) Two inconspicuously coloured Cerambycid beetles 12 to 14 mm. long (*Elaphidion guttiventre* Chev.) were put into the cage at the same time as the bugs. The beetles were both eaten the first day; the bugs were all alive and active after five days, during which the lizards were not fed. At the end of this time several roach nymphs were put into the cage and the lizards snapped them up at once, seeming to be very hungry.

Water was kept in the cages, but the lizards drank very little. Once, however, I saw one licking with its short tongue at drops of water on the cage floor.

Anolis sagrei, then, is abundant throughout the year in the same habitat as *Thonalmus*, hunts in shrubbery, is diurnal, hunts by eye, is insectivorous and eats a variety of insects including various beetles the size of *Thonalmus*, but is not completely indiscriminate. In short, it possesses the characteristics to be expected of a mimefactor concerned in *Thonalmus* mimicry. And it adapts itself well to captivity.

Thonalmus spp. (Lycidae).

There are three species of *Thonalmus* in Cuba. *T. suavis* (J.-D.) and *T. aulicus* (J.-D.) are common at Soledad and were used in my experiments. *T. amabilis* (J.-D.) is not yet known from Soledad but may occur there. The three species are almost identical in appearance. The genus as a whole rather than a single species must be considered the model for any mimics which occur. The great similarity of the three Cuban species of *Thonalmus* may possibly be an example of Müllerian mimicry, but on the other hand it may be due merely to their close interrelationship.*

Mr. Fischer's beautiful figures of a large female and a small male of *Thonalmus suavis* (Pl. 1, figs. 1, 2) make a detailed description of the appearance of the insects unnecessary. The ventral surface of the body, and also the dorsal surface of the abdomen which is exposed in flight, are bright red or orange. The inner wings are dusky with about the basal third yellowish. The legs vary in colour from black with red at the bases of the femora to red with only the tarsi black; the legs may, therefore, appear superficially either black or red. In size, *Thonalmus* vary from about 6 to 13 mm. There is a good deal of variation also in details of form (the elytra are often less flaring than in the individuals figured) and some variation in pattern and colour. Almost all of this variation, including that in size, is individual rather than sexual or specific.

As I have said, these beetles frequent all sorts of bushy and overgrown places near Soledad. In spring and summer they are, if not the most abundant, certainly among the most conspicuous insects in their habitat.† Almost every individual of *Anolis sagrei* must encounter many of them during its lifetime.

* The following key to the Cuban species of *Thonalmus* is adapted from Leng and Mutchler (1922, p. 419).

1. Outer and middle costae (not counting thickened margins) of each elytron united to form a connecting curve near apex; (antennae of both sexes merely serrate) *suavis*
– Elytral costae not connected apically 2
2. Segments 4 to 10 of male antennae each with lower apical angle produced to form a process about ½ as long as the axial portion of the segment; antennae of female merely serrate . . . . . *amabilis*
– Antennae of both sexes merely serrate . . . . . *aulicus*

(The sexes of *Thonalmus* may be distinguished by the form of the penultimate ventral segment of the abdomen, which is truncate in the female, but so deeply emarginate at apex in the male that it appears as a pair of lobes at the sides of the last segment.)

† Some idea of the abundance and conspicuousness of the *Thonalmus* may be had from the following counts, made along 570 yards of a *callejón* (a trail for horsemen and cattle between two bushy, overgrown fencerows) just east of the Soledad laboratory. In making the counts I walked along the trail in one direction only, without stopping, and without looking under leaves or on the far sides of bushes or attempting otherwise to find hidden individuals. 26 April, 10 a.m. (clear, foliage dry, breeze faint): counted 22 *Thonalmus*, 3 of them flying. 27 April, 8 a.m. (clear, foliage damp, some wind): 13 *Thonalmus*, 1 flying. 28 April, 5 p.m. (clear, foliage dry, windy): 9 *Thonalmus*, all clinging to leaves, apparently to avoid being carried away by the wind.

During the dry season the beetles seem somewhat less common, but not rare. In favourable country they range from sea level up to at least 3000 ft. altitude in the mountains.* They are semi-gregarious and frequently occur in loose aggregations, but single individuals also are frequent. Except when they are driven to cover by wind or rain, they are active during the day, resting and crawling, as a rule, on the outer twigs of shrubs, and often flying in sunlight. They are usually inactive at night, although occasional specimens have been collected at lighted windows at night at Soledad.

The beetles are deliberate in their movements. They crawl rather than run. They fly slowly and, in wind, driftingly, with antennae and elytra extended, planing and circling broadly like most other beetles.

Thonalmus are very inoffensive insects. They are soft and weak, without spines, with small mandibles which, so far as I have observed, they never use for defence. They do, however, exude a pink fluid when they are handled. The fluid may appear from many different parts of the body. For instance, I have seen it come from between the abdominal segments ventrally, from lateral and ventral sutures of the thorax, from between the trochanter and femur of a leg, and, most frequently, from both the inner and outer margins of the elytra.

Since this fluid is so widely distributed within the body, it seems safe to say that it is the insects' blood. The bleeding is not, strictly speaking, auto-haemorrhage, for a certain amount of external pressure is necessary to start it. If a beetle is held by an antenna alone, no bleeding occurs no matter how actively the insect struggles. On the other hand, a surprisingly light pressure will rupture some membrane or the edge of an elytron and start bleeding, or perhaps will give the insect purchase to rupture itself.

The bleeding of *Thonalmus* is a much more complicated phenomenon than might at first be supposed. The elytra seem especially adapted for it. Both the inner and outer margins are slightly swollen, hollow, and tube-like. The outer margin, which is perhaps the part of the insect most likely to be damaged in a struggle, is especially swollen. When an uninjured specimen of *Thonalmus suavis* was held by an antenna and the apical quarter of one elytron clipped off with scissors, blood at once flowed from both inner and outer marginal ducts, and in about a minute formed two very large drops, the larger appearing from the outer marginal duct. The blood did not squirt out, neither did it just ooze, but flowed steadily as if under pressure. When, after bleeding had stopped, the second elytron was cut in the same way, about the same amount of blood flowed as from the first. I was convinced that more blood flowed from each elytron than could possibly have been contained in the elytral ducts at the instant of cutting, so that blood must have flowed from the insect's body into the elytra during the bleeding.

This experiment was repeated using, instead of living beetles, some just killed in a cyanide jar. No bleeding occurred. Some blood could be squeezed from the elytra with forceps, but only a fraction of the amount which flowed from living specimens. The experiment was repeated again with lightly etherised specimens (they were immobile only two or three minutes), and again no bleeding followed the cutting. There was no bleeding, either, when the Lycids resumed activity, but perhaps by that time some sort of clotting had taken place.

* I have taken *Thonalmus suavis* and *T. aulicus* at 3000 ft. in the Trinidad Mts., Sta. Clara Prov.; *T. suavis* at the same altitude in the Cobre Range, Oriente Prov.; and all three Cuban *Thonalmus* between 3000 and 3500 ft. in the Purial Range, Oriente.

The free haemorrhage of these insects, then, is not merely the oozing of blood from injured tissue; it is voluntary, or at least depends on a condition of excitement. The elytra seem actually to be structurally adapted to facilitate free haemorrhage, and I have already commented on the very slight pressure which will start bleeding and on the surprising quantity of blood produced. The loss of even several drops of blood seems not to incommode the beetles very much. If they are not otherwise injured, they crawl and fly apparently normally soon after losing it. All this leads to the conclusion that free haemorrhage is actually a protective adaptation.

As a matter of fact, the *Thonalmus*' blood is not offensive to human senses.* I tested it by rubbing it first on thin skin between my fingers, then on my lips, and finally on my tongue. The taste and odour are very mild, reminiscent of crushed lettuce, and I noticed no after effects. Nevertheless *Anolis sagrei* consistently refuses to eat *Thonalmus*. There is no need to describe all my experiments in detail. Briefly, from two to four living Lycids were kept in cages from 24 to 27 April, 2 to 7 May, and 17 to 21 August, together with a total of four different male and one female *Anolis*. During these periods the lizards were sometimes supplied with acceptable food, sometimes left unfed for one or two days. Of acceptable insects they ate, besides a few roaches, 22 plainly coloured beetles as large as or slightly larger than the Lycids while the latter were in the cage.† Not one Lycid was eaten, nor, so far as I observed, was one ever attacked by an *Anolis*.

To clinch the matter, on 21 August, an experiment was tried with a male lizard which had become somewhat accustomed to handling. First the lizard was held down by hand and a small, green, Geometrid-like larva was placed in its mouth, but not pushed down its throat. The lizard was then carefully released. It waited motionless for a few seconds and then swallowed the larva. The lizard was recaptured and a *Thonalmus* placed in its mouth. The beetle was shaken out at once by an energetic side-to-side motion of the lizard's head. Afterwards the lizard ran its blunt tongue over its lips as if cleansing them. About five minutes later another small larva was given and swallowed; then two more Lycids were emphatically rejected.

These observations and experiments demonstrate, I think, not only that the *Thonalmus* are not attacked by *Anolis sagrei*, which is perhaps the most important insectivorous animal in their environment, but also that the beetles are protected as a result of their own characteristics and adaptations, not because they resemble anything else. It practically follows that the bright colouration of the beetles, whatever its origin, acts as a warning or aposematic colouration which the lizards learn to respect. According to the theory of mimicry, such colouration should be worth imitation among insects of the same size and proportions as the Lycids, and it is in fact repeated more or less faithfully in several unrelated families of Cuban beetles.‡

* Marshall (1902, p. 518) describes the fluid emitted by certain African LYCIDAE as "a very strong-smelling white fluid."

† Of the beetles eaten, 11 were ELATERIDAE (*Conoderus bifoveatus* Beauv.) and 11 CERAMBYCIDAE (6 different species).

‡ The resemblance of beetles of various unrelated families to LYCIDAE has often been noticed. See, for example, Marshall (1902, pp. 515–518) for Lycid mimicry in South Africa; Shelford (1902, pp. 267–272) for Lycid mimicry in Borneo; Gahan (1913) for examples from Burma, East Africa, and South America; and Arrow (1928) for some additional examples from South America. See also Jones (1932, pp. 358–359) for the relative unacceptability to birds of the North American Lycid *Calopteron reticulatum* (F.).

The Lycid-like Beetles.

The following is a list of the Cuban beetles in the Museum of Comparative Zoölogy, Harvard, which show a more or less close resemblance to *Thonalmus*. I have added what information I possess concerning the insects' habits and their occurrence with or near *Thonalmus*. I am indebted for identifications of material to Mr. A. J. Mutchler (Lampyridae and Cantharidae), Mr. W. S. Fisher (Cerambycidae) and Mr. E. D. Quirsfeld (Elateridae).

Callopisma spp. (Lampyridae): There are at least three Cuban species of fireflies of this genus which resemble *Thonalmus* in a general way, being yellow or orange with antennae and apical half of elytra black. However, the resemblance is imperfect in various details, and all of the species of *Callopisma* with which I am acquainted are forest dwellers and are not likely to occur in the same habitat as *Thonalmus*.

Tytthonyx spp. (Cantharidae, formerly Telephoridae): Three recently described Cuban species of *Tytthonyx* (Mutchler 1937) are superficially strikingly similar to small individuals of *Thonalmus*. The *Tytthonyx* differ from *Thonalmus* in having the elytra abbreviated, but the inner wings are black and project beyond the elytra, so that the beetles appear at a glance to have long elytra which are red with black apices. The ground colour of the *Tytthonyx* varies from orange to red. The body below and also the dorsal surface of the abdomen are bright orange or red except that the last two or three abdominal segments are black. In size, the species of *Tytthonyx* vary from about $4\frac{1}{2}$ to 8 mm. In most lights, the resemblance to *Thonalmus* is greater than appears in Plate 1, except that the blue areas of *Thonalmus* are black in *Tytthonyx*. *Tytthonyx rubidus* Mutch. (Pl. 1, fig. 3) and *T. darlingtoni* Mutch. were taken in the Trinidad Mts., Sta. Clara Prov., at about 3000 ft. altitude, in May. They were active by day on small flowering trees on the borders of woodland, in company with *Thonalmus*. *T. rutilis* Mutch. was taken at Soledad in May on flowers of the Guásima tree (*Guazuma ulmifolia* Lam.), also by day and in company with *Thonalmus*.

Copidita thonalmus Darl. (Oedemeridae) (Pl. 1, fig. 4): This recently described insect (Darlington 1936) is strikingly similar to *Thonalmus* in colour; the differences in form are not very obvious superficially. The only specimen I have ever taken was on a flowering tree in the Trinidad Mts., at 3000 ft. altitude, in May, in company with *Thonalmus* and *Tytthonyx*. The Museum of Comparative Zoölogy, Harvard, possesses five other specimens from the collection of the Tropical Plant Research Foundation labelled as collected at Jaronú (Camagüey Prov.), 27 May, " on weeds," by L. C. Scaramuzza.

Anoplischius venustus (J.-D.) (Elateridae) (Pl. 1, fig. 5): Whether or not this insect would be called *Thonalmus*-like would depend on the conditions under which it was seen; it is less like the Lycids than any other of the beetles figured. I have taken the species occasionally at Soledad in May and June, sometimes on Guásima flowers in company with *Thonalmus*. The Elaterid appeared to be diurnal.

Platycrepidius schaumi (Cand.) (Elateridae): Superficially similar to the preceding species except that it is relatively broader and more parallel, with much shorter antennae and less black on the elytral apices. I have never seen this species in life, but the Museum possesses a specimen from Jaronú, 27 May, collected by L. C. Scaramuzza " on *Solanum*," and Mr. Quirsfeld wrote me that he has seen specimens from near Havana and from Camagüey taken in May and July.

Calocosmus venustus (Chev.) (Cerambycidae, Lamiinae) (Pl. 1, fig. 6): This species measures, in the Museum series, from 9·5 to 11·5 mm. The body below is orange (except that the metathorax is dusky) and so is the dorsal surface of the abdomen. The Cerambycid is more convex, with more prominent humeri and longer antennae than *Thonalmus*, but the resemblance to the latter is striking. The black humeral spots of the Cerambycid increase rather than decrease the likeness, for they tend to block out the too prominent humeri. This beetle is rare near Soledad, but the Museum has one from there dated 8 June (*G. Salt*) and I took three in May. One of them was flying (by day) on the edge of open woods (the Limones *Seboruco*) when I first saw it; there were *Thonalmus* flying within a few yards. Between 9 and 14 May I found eight more specimens on bushes and grass blades in a scrubby ravine, also a habitat of *Thonalmus*, near Buenos Aires in the Trinidad Mts., which are only a few miles from Soledad, at about 3000 ft. altitude. These individuals, too, were more or less active by day. The Museum has specimens also from Jaronú, 28 May, and Baraguá, 3 July (L. C. Scaramuzza).

Calocosmus dimidiatus (Chev.) (Cerambycidae, Lamiinae): Very similar to *C. venustus*, but averaging a trifle smaller and more slender, with the apices of the elytra black instead of blue and the antennae more obviously banded with yellow. The different colour of the elytral apices makes this somewhat less *Thonalmus*-like than the preceding species. *C. dimidiatus* is not yet known from Soledad. I took a specimen in the Trinidad Mts. (May) and one in the Purial Range, Oriente Prov. (July), but I do not remember anything about their habitat or behaviour.

Trichrous divisus Chev. (Cerambycidae, Cerambycinae) (Pl. 1, fig. 7): This insect varies from 7·5 to 12 mm. in length. The lower surface and the dorsum of the abdomen are red. In life this is the most strikingly *Thonalmus*-like beetle that I know, although its antennae are longer than those of the Lycid. It has not been found at Soledad, but between 9 and 14 May I took nearly 30 specimens near Buenos Aires, Trinidad Mts., between 3000 and 3500 ft. altitude. The insects were active by day, mating and flying, in coffee lots and partly cleared places and on flowers of an unidentified tree. *Thonalmus* was frequently found in the same neighbourhood.

Heterops dimidiata (Chev.) (Cerambycidae, Cerambycinae) (Pl. 1, fig. 8): About the size and form of the preceding species. The colouration is nearly the same except that the outer halves of the elytra are black instead of blue. The present species is less *Thonalmus*-like than the preceding, of course, although the superficial resemblance is fairly good. My first specimens of *H. dimidiata* were found in the north-western foothills of the Trinidad Mts. on 30 April and 1 May. They were on guava flowers (*Psidium Guajava* L.) in hedgerows beside the trail in cleared land. On 6 May I found additional specimens on flowers of *Croton lucidus* L. beside a trail in an overgrown clearing in the Guabairo *Seboruco*, on the Soledad Estate. On both occasions the insects were active by day and were in habitats where *Thonalmus* occurred.

Trichrous pilipennis Chev. (Cerambycidae, Cerambycinae) (Pl. 1, fig. 9). From 6 to 8 mm. long. The body below, and the dorsal surface of the abdomen, are red. In spite of its slightly more slender form, slightly longer antennae, and more shining and pubescent surface, *T. pilipennis* is very much like a small *Thonalmus* in general appearance. I found the species active by day at the same times and places as the preceding, and took it also on Guásima flowers on the edge of the Limones *Seboruco* near Soledad, in May, in places where *Thonalmus* was common.

Trichrous dimidiatipennis (Chev.) (CERAMBYCIDAE, CERAMBYCINAE): This is a larger and broader species than *T. pilipennis*, less distinctly pubescent, but coloured nearly the same. It is rather more *Thonalmus*-like than *T. pilipennis*. I took a single specimen at about 3000 ft. altitude on the Cobre Range, Oriente Prov., in July, but I do not remember the circumstances of capture. The species is not yet known from Soledad.

None of these *Thonalmus*-like beetles can possibly be either a predator or a guest of the Lycids. If mimicry is involved, therefore, it apparently must be simply protective, of the Batesian or Müllerian type. For reasons given above, the Lycid-like LAMPYRIDAE are probably not mimics at all. The three species of CANTHARIDAE may well be mimics. CANTHARIDAE (TELEPHORIDAE) occur with LYCIDAE in apparently mimetic associations in other parts of the world (see papers cited above, p. 688). Whether the Cuban forms are Müllerian or Batesian mimics can be determined only by experiment. Poulton (see Marshall 1902, p. 393) included the TELEPHORINAE (= CANTHARIDAE of the present paper) in his list of specially defended Coleoptera, and Gahan (1913, p. 34) stated that, in his opinion, almost the whole of the TELEPHORIDAE possess secretory glands which secrete a protective liquid—evidently a very different mechanism from the free haemorrhage of *Thonalmus*. On the other hand, however, Jones (1932, tables on pp. 352 and 353) finds that, although CANTHARIDAE have a low acceptability rating, they sometimes are taken by birds. It seems to me far from certain that all CANTHARIDAE are inherently distasteful. The beautiful Oedemerid which resembles *Thonalmus* so strikingly is probably a mimic, of the Müllerian type. OEDEMERIDAE often resemble and are associated with LYCIDAE (see not only papers already cited, but also Champion 1890, p. 130, under genus *Sisenes*, and under various species of the genus). I could not get specimens of *Copidita thonalmus* for experiment, but I did try the less brightly coloured *C. testaceicollis* (J.-D.) and *Anolis sagrei* rejected it.* The ELATERIDAE and CERAMBYCIDAE, on the other hand, are families which are frequently eaten by *Anolis*. I have, unfortunately, no experimental data on the *Thonalmus*-like ELATERIDAE, but I was able to experiment with four species of CERAMBYCIDAE.

CAGE EXPERIMENTS.

Living specimens of the following four species of CERAMBYCIDAE were used in the experiments: *Calocosmus venustus* (Chev.) (Pl. 1, fig. 6), *Trichrous divisus* Chev. (fig. 7), *Heterops dimidiata* (Chev.) (fig. 8), and *Trichrous pilipennis* Chev. (fig. 9). All of them resemble *Thonalmus* fairly closely, not only when the elytra are closed, but, perhaps even more, when the wings are spread, for the upper surface of the abdomen is red like that of *Thonalmus*, and the inner wings are like those of the Lycids too, dusky with yellowish bases. The Cerambycids are somewhat more active than the Lycids, but their movements are not otherwise dissimilar. The flight of the Cerambycids, which I observed for the four species in the screened porch of the Soledad Laboratory, is a little more rapid than that of the Lycids, but has the same Coleopterous planing and circling qualities. There is, in short, no character of either appearance or behaviour which immediately distinguishes the Cerambycids from *Thonalmus*.

* When three specimens of *Copidita testaceicollis* (J.-D.) were put into a cage with two male and one female *Anolis sagrei*, the female and one of the male lizards rushed at them. The male stopped short without touching the beetles. The female seized one but released it instantly, and then rubbed the sides of its mouth on the cage floor and licked at its lips.

The following chronology summarises my cage experiments:

2 *May:* Placed in cage (described above) with 2 male and 1 female *Anolis sagrei* the following: 4 *Thonalmus aulicus*, 2 *Heterops dimidiata*, and 2 *Trichrous pilipennis*.

3 *May:* All beetles alive and active, except 1 *Trichrous*.* At 10 a.m. put into cage 4 plainly coloured CERAMBYCIDAE (2 *Elaphidion guttiventre* Chev., 1 *Leptostylus incrassatus* (Klug), and 1 *Eupogonius pilosulus* (Chev.)). A male *Anolis* ate one of the *Elaphidion* within a few minutes; at 11.30 the same *Anolis* ate the other *Elaphidion*.

4 *May:* *Eupogonius* eaten.

5 *May:* *Leptostylus* eaten.

6 *May:* Put in cage 2 more plain CERAMBYCIDAE (1 *Ataxia spinicauda* Schffr. and 1 *Cyllene crinicornis* Chev.). A male *Anolis* seized and ate the *Ataxia* about one second after it was put in, and the *Cyllene* was eaten almost equally quickly.

7 *May:* Put in 4 more plain CERAMBYCIDAE (3 *Elaphidion guttiventre*, 1 *E. nanum* (Fab.)) at 6.30 a.m. By evening all 4 had been eaten. Experiment closed. The 4 *Thonalmus*, 2 *Heterops*, and 1 *Trichrous* were all alive and active.

16 *May:* Placed in cage with 2 male *Anolis sagrei* the following: 1 *Calocosmus venustus* and 2 *Trichrous divisus*.

17 *May:* Put into cage 3 plainly coloured ELATERIDAE (*Conoderus bifoveatus* Beauv.), which were eaten within 15 minutes.

18 *May:* *Calocosmus* dead on floor of cage, but apparently not killed by lizards, for not crushed nor broken. Put into cage 5 more ELATERIDAE (same species), of which 4 were eaten at once and the other later.

19 *May:* No change.

20 *May:* No change.

21 *May:* Put 2 plain CERAMBYCIDAE (1 *Elaphidion guttiventre*, 1 *Leptostylus incrassatus*) into cage.

22 *May:* No change.

23 *May:* *Elaphidion* eaten, *Leptostylus* not.† Both *Trichrous* alive and active. Experiment closed.

In these experiments seven specimens of four species of *Thonalmus*-like CERAMBYCIDAE were caged for periods of up to a week with *Anolis sagrei*, sometimes with and sometimes without *Thonalmus* in the cage. In no case did the lizards eat or, so far as I observed, show any interest in the *Thonalmus*-like species. *Heterops dimidiata*, with black tipped elytra, survived as well as the blue tipped species which resemble *Thonalmus* more closely. While the *Thonalmus*-like CERAMBYCIDAE were in the cage unmolested, the lizards did eat eleven plainly coloured specimens of six rather diverse species (some CERAMBYCINAE, some LAMIINAE) of the same family. They refused no plainly coloured species and, at the end of the experiments, had failed to eat only one

* This specimen disappeared, apparently escaping through a small crack accidentally left in one corner of the cage. In order to make sure that it had not been eaten, I broke up in alcohol and examined under a binocular microscope all lizard excrement found in the cage for several days afterwards. The exoskeletons of beetles pass through the *Anolis*' digestive tract almost unchanged, frequently with even the scales and pubescence intact. I was able to find elytra of all the beetles I knew had been eaten, but not of the *Trichrous*.

† Note that a specimen of this species had been eaten 5 May, after some delay.

plainly coloured individual. At the same time they ate also eight plainly coloured ELATERIDAE.

There is nothing, so far as I can find, in the structure of these *Thonalmus*-like CERAMBYCIDAE to make them less acceptable food than the plainly coloured species—no difference in size or hardness or spinosity—nor do the *Thonalmus*-like forms exude a defensive fluid. Apparently only their great similarity to *Thonalmus*, which the lizards will not touch, will account for their survival in the lizard cages.

DISCUSSION.

The preceding experiments are not above criticism, but, added to what has been learned about *Anolis sagrei* and the species of *Thonalmus*, they show pretty clearly that the Lycid-like appearance of the Cerambycids is due to mimicry. It is probably Batesian mimicry, but this is not absolutely sure. The edibility of the mimetic forms ought to be tested by artificial feeding, by placing the beetles in *Anolis*' mouths. I could not get living specimens of the beetles when I wanted to make this test. The majority of CERAMBYCIDAE the world over appear to be relatively edible insects, and this is probably one of the reasons why so many of them have come to mimic wasps, bees, ants, and protected families of beetles. However, Jones (1932, pp. 357–358, 367–369) found that the North American Cerambycid *Tetraopes tetraophthalmus* (Forst.) is relatively unacceptable to birds, apparently because it feeds on an acrid milkweed, and other exceptional CERAMBYCIDAE may be similarly unappetising.

As a matter of fact, although I have made the customary distinction between Batesian and Müllerian mimicry in the preceding pages, it seems to me that the distinction is not very important. A Batesian mimic is supposed to be rare and edible; a Müllerian mimic, common and inedible. Commonness and edibility, however, are relative rather than absolute matters. Different organisms range all the way from very common to very rare, and there is complete intergradation, too, between organisms which are entirely acceptable as food and those which are unacceptable (see Jones' tables, 1932). Moreover, commonness and acceptability are not always correlated. All sorts of intergrades between typical Batesian and typical Müllerian mimicry might, therefore, be expected, and do actually occur.

In Cuba, for example, the existence together of such a striking, common, and unpalatable genus as *Thonalmus* and such a genus of insectivorous lizards as *Anolis* (there are about twenty species of *Anolis* in Cuba, all more or less diurnal and arboreal), together probably with other mimefactors, forms an ideal setting for mimicry. In this setting beetles of various families have evolved a colour pattern more or less like that of *Thonalmus*, presumably through the action of natural selection. None of the mimetic forms is common enough to be of much value to *Thonalmus* in Müllerian mimicry, nor is there any reason to think that *Thonalmus* has converged with any of them. The fact that some of the mimics appear to be inherently less edible than others does not change the fact that *Thonalmus* is the model and the other beetles mimics. Under these conditions the customary distinction between edible Batesian and inedible Müllerian mimics does not mean very much.

I have no intention of arguing the pros and cons of the mimicry theory here. It is hard to see how any entomologist who has had field experience in the tropics can doubt that mimicry occurs commonly among insects. On the other hand, it seems to me that proponents of mimicry theories still make altogether too many sweeping generalisations. I do not intend, either, to

review the literature of mimicry; my bibliography will be limited to papers cited in the text. Carpenter and Ford (1933) have recently published a small book, appropriately dedicated to Prof. E. B. Poulton, reviewing the subject of mimicry and listing important references.

Future Study at Soledad.

There is, as I have said at the beginning of this paper, an unrivalled opportunity for study of mimicry and related phenomena at the Soledad laboratory. I hope to continue experiments myself from time to time, but there is more to be done than any one person can hope to do. The work can probably best be carried on in the spring and early summer, from May to July, when insect life is most abundant. At other seasons, some of the *Thonalmus* mimics, rare at best, are entirely unobtainable.

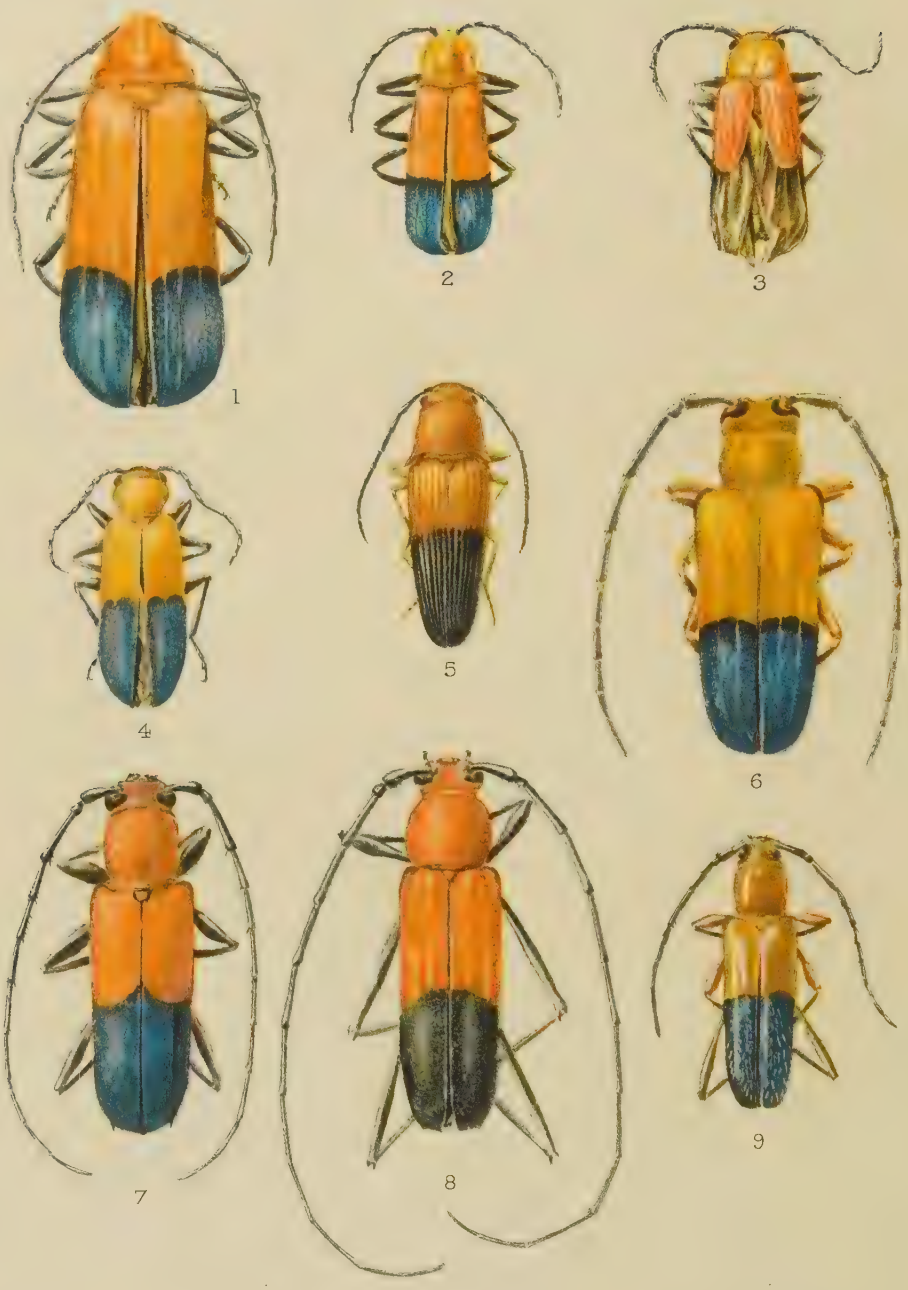
All insectivorous organisms—birds, lizards, insects, spiders—which may be mimefactors should be investigated, not only those which feed on beetles, but others. For example, in connection with "myrmecoidy," it is necessary to know what organisms prey on ants and what do not. It is not enough to know that some lizards eat some ants; it is necessary to know what lizards eat what ants and how readily.

It is necessary to know, too, something of the habitat and habits of each predator, and it would be very interesting to know the life histories of some of them. For instance, in *Anolis sagrei* not only should more be found out about the food of adults, but the behaviour and food of the young should be studied. The conditioning of young individuals, probably by trial and error, to different sorts of food might be a refreshing change of study from rats or the sexual habits of simians for some animal psychologist. Do the lizards learn to reject one species of insect at a time, or do they reject by genera or families? Do they keep trying one species of Hemiptera after another, or do a few trials teach them to reject all true bugs? Will a few unpleasant experiences with *Thonalmus* result in the lizards rejecting all bright red and blue or red and black insects, or only strikingly *Thonalmus*-like forms? This sort of information is essential to determine the significance of imperfect resemblances.

In *Thonalmus*, the life histories of the species might be investigated. The larvae of Lycidae usually live in decaying wood, but not much is known about most of them. The physical adaptations of the adults for free bleeding as well as the constitution of the blood should be studied.

My experiments with *Thonalmus* and its mimics should be repeated and amplified. Results may eventually prove to be statistical rather than, as in my experiments, absolute. More of the *Thonalmus*-like beetles should be tested, especially those in which the resemblance is relatively imperfect. The edibility of the *Thonalmus*-like species should be tested by artificial feeding, and interesting experiments could be devised with artificially coloured beetles and with edible species smeared with *Thonalmus*' blood.

After *Thonalmus* mimicry, the examples of myrmecoidy described by Myers and Salt (1926) are probably the most promising phenomena for investigation. But whatever the problem, the outline on p. 682 ought to be satisfied.



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THONALMUS AND *THONALMUS*-LIKE BEETLES FROM CUBA.

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Explanation of Plate 1.

Thonalmus *and* Thonalmus-*like Beetles from Cuba.*

(all figures about × 4.)

Fig. 1. *Thonalmus suavis* (J.-D.); large female from Soledad, near Cienfuegos, Santa Clara Prov., Cuba (Lycidae).

2. *Idem*; small male from Buenos Aires, Trinidad Mts., Santa Clara Prov., Cuba (Lycidae).

3. *Tytthonyx rubidus* Mutch.; female from Buenos Aires, Cuba (Cantharidae).

4. *Copidita thonalmus* Darl.; from Jaronú, Camagüey Prov., Cuba (Oedemeridae).

5. *Anoplischius venustus* (J.-D.); from Soledad, Cuba (Elateridae).

6. *Calocosmus venustus* (Chev.); from Buenos Aires, Cuba (Cerambycidae, Lamiinae).

7. *Trichrous divisus* Chev.; from Buenos Aires, Cuba (Cerambycidae, Cerambycinae).

8. *Heterops dimidiata* (Chev.); from north-western foothills of the Trinidad Mts., Cuba (Cerambycidae, Cerambycinae).

9. *Trichrous pilipennis* Chev.; from north-western foothills of the Trinidad Mts., Cuba (Cerambycidae, Cerambycinae).

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ERRATA.

p. 190, line 4, for "var. *uniformis*" read "var. *concolor* Grib."
p. 190, line 15, for "*colobopterous*" read "*colobopterus*."